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Published in:
Ecology

DOI:
10.1002/ecy.1954

Publication date:
2017

Document Version
Peer reviewed version

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Article type : Articles

The importance of species identity and interactions on multifunctionality depends on how ecosystem functions are valued

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Running title: Optimizing multifunctionality

Abstract

Studies investigating how biodiversity affects ecosystem functioning increasingly focus on multiple functions measured simultaneously ('multifunctionality'). However, few such studies assess the role of species interactions, particularly under alternative environmental scenarios, despite interactions being key to ecosystem functioning. Here we address five questions of central importance to ecosystem multifunctionality using a terrestrial animal system: 1) Does the contribution of individual species differ for different ecosystem functions?; 2) Do inter-species interactions affect the delivery of single functions and multiple functions?; 3) Does the community composition which maximises individual functions also maximise multifunctionality?; 4) Is the functional role of individual species, and the effect of interspecific interactions, modified by changing environmental conditions?; and 5) How do these roles and interactions change under varying scenarios where ecosystem services are weighted to reflect different societal preferences? We manipulated species' relative abundance in dung beetle communities and measured 16 functions contributing to dung decomposition, plant productivity, nutrient recycling, reduction of greenhouse gases, and microbial activity. Using the Multivariate Diversity-Interactions framework, we assessed how changes in species identity, composition, and interspecific interactions affected these functions in combination with an environmental driver (increased precipitation). This allowed us to identify key species and interactions across multiple functions. We then developed a Desirability Function Approach to examine how individual species and species mixtures contribute to a desired state of overall ecosystem functioning. Species contributed unequally to individual functions, and to multifunctionality, and individual functions were maximised by different community compositions. Moreover, the species and interactions important for maintaining overall multifunctionality depended on the weight given to individual functions. This combination of methodological approaches allows us to resolve the interactions and indirect effects among species that drive ecosystem functioning, revealing how multiple aspects of biodiversity can simultaneously drive

ecosystem functioning. Optimal multifunctionality is therefore context-dependent, and is sensitive to the valuation of services. Our results highlight the importance of a multifunctionality perspective for complete assessment of species' functional contributions.

Keywords: biodiversity, ecosystem function, multivariate diversity-interaction model, dung beetle, environmental perturbation, ecosystem services, extinction scenarios, Desirability Function Approach, complementarity, dominance, species interactions, multifunctionality

1. Background

Species-rich communities have been shown to deliver enhanced ecosystem functions and services in both natural and human-modified ecosystems (Schwartz et al. 2000, Balvanera et al. 2006, Proulx et al. 2010, Cardinale et al. 2012, Hooper et al. 2012, Allan et al. 2015, Butterfield et al. 2016). Early studies of the links between biodiversity and ecosystem functioning (BEF) considered a limited range of biodiversity metrics (mostly species richness) and ecosystem functions (particularly productivity) (Jonsson et al. 2002, Loreau et al. 2002, Smith and Knapp 2003, Bell et al. 2005). More recently, there has been an emphasis on extending BEF studies to wider measures of biodiversity – including functional diversity, biotic interactions, and the abundance of particular taxa (Cardinale et al. 2012, Oliver et al. 2015) – and to wider measures of functioning – including ecosystem multifunctionality and ecosystem services (Hector and Bagchi 2007, Isbell et al. 2008, Maestre et al. 2012, Duncan et al. 2015).

Species within a community often have varying impacts on different ecosystem functions. Thus, the number of species needed to sustain multiple functions simultaneously can be substantially higher than the number required for any single function (Hector and Bagchi 2007, Isbell et al. 2008, Maestre et al. 2012). This situation might be exacerbated in temporally- or spatially-heterogeneous environments, because the species critical to delivering functions will then

vary in both space and time (Isbell et al. 2008). High species richness, heterogeneous response traits, and functional redundancy can buffer multi-functionality through an 'insurance' or 'portfolio' effect (Gamfeldt et al. 2008, Isbell et al. 2008, Lefcheck et al. 2015, Oliver et al. 2015, Perkins et al. 2015), but past studies have focused on plant or microbial communities. While there are recent studies focussing on animal diversity-functioning relationships (e.g. Wagg et al. 2014, Gagic et al. 2015, Winfree et al. 2015, Dee et al. 2016), there remain critical knowledge gaps in understanding the combined impacts of animal communities and of environmental perturbations on ecosystem multifunctionality (Allan et al. 2015, Duncan et al. 2015, Soliveres et al. 2016b).

In this paper, we explore the effects of north European dung beetles (Coleoptera: Scarabaeidae) species identity, abundances, and interspecific interactions on multiple measures of ecological functioning. We also investigate whether these effects differ under changing environmental conditions (ambient and elevated precipitation), and varying scenarios where ecosystem services are weighted to reflect different societal preferences. We focus on dung beetle because they are important contributors to a range of ecosystem functions and services in many terrestrial habitats (Nichols et al. 2008). Dung beetles exploit the faeces of vertebrates for feeding and breeding, and are a functionally important invertebrate guild in many terrestrial ecosystems (see Nichols et al. 2008 for review). Key ecological functions mediated by dung beetles include nutrient recycling (Bang et al. 2005, Yamada et al. 2007), secondary seed dispersal (Andresen 2002, D'hondt et al. 2008), reduction of greenhouse gas emissions (Penttilä et al. 2013, Slade et al. 2016), and the facilitation of microbial activity through bioturbation (Slade et al. 2015). The services provided by dung beetles were recently valued at £367 million annually in the UK alone (Beynon et al. 2015). However, dung beetles are also sensitive to anthropogenic environmental change, potentially placing these valuable ecosystem services at risk. For example, in Finland, of 47 native

species more than half are extinct, endangered or near threatened (Roslin et al. 2014), with poorly-documented consequences for ecosystem functions and services.

We measured 16 functions contributing to dung decomposition, plant productivity, nutrient recycling, reduction of greenhouse gases, and microbial activity. Differences in breeding behavior among dung beetle species (Figure 1) are expected to result in contrasting species contributions to individual functions (Slade et al. 2015, Slade and Roslin 2016). Within the dung pat, species will exploit slightly different parts of the dung (Holter 1982) using different breeding strategies, and will have preferences for dung of varying ages (Gittings and Giller 1997, 1998). Interspecific competition among dung beetle species is limited in Northern Europe (Finn and Gittings 2003). Thus, we expect the activity of different species to positively affect or complement each other, and complementarity in resource use to generate an overall positive correlation between species richness and functioning (Slade et al. 2007, Slade and Roslin 2016) (Figure 1). In addition, we expect increased species richness to generate an 'insurance' or 'portfolio' effect, where more diverse dung beetle communities may sustain higher functional rates under more diverse – and potentially changing – environmental conditions (cf. Beynon et al. 2012, Slade and Roslin 2016).

To explore the proposed interactions between diversity effects and environmental conditions, we experimentally manipulated precipitation. Over the coming decades, summer rainfall is predicted to increase and become more variable across northern Europe (Jenkins et al. 2009, Jylhä et al. 2009). Increased moisture can increase the activity and reproductive capacity in temperate dung beetles (Vessby 2001), which may lead to changes in the interactions among species. We also predicted that increased moisture would have positive direct effects on most ecosystem functions, increasing dung decomposition, plant productivity, nutrient recycling and

microbial activity. However, increased moisture also increases greenhouse emissions (Levy et al. 2012, Pilegaard 2013), negatively affecting this function from an ecosystem services perspective.

Previous analytical tools have not addressed the importance of species interactions and multiple mechanisms for driving ecosystem functions across different contexts. We apply the newly-developed Multivariate Diversity-Interactions framework (Dooley et al. 2015) for ecosystem multifunctionality to this model system. In combination, we develop a novel Desirability Function Approach to measure the contribution of individual species and interactions among species, to a desired state of overall ecosystem functioning. The approach allows us to capture the extent to which precipitation modifies both species-specific functional efficiency and interactions among species, and to address the following questions: 1) Does the contribution of individual species differ for different ecosystem functions?; 2) Do inter-species interactions affect the delivery of single functions and multiple functions?; 3) Does the community composition which maximises individual functions also maximise multifunctionality?; 4) Is the functional role of individual species, and the effect of interspecific interactions, modified by changing environmental conditions?; and 5) How do these roles and interactions change under varying scenarios where ecosystem services are weighted to reflect different societal preferences?

2. Materials and methods

2.1. Study system

We assembled dung beetle communities comprising one to four species, selected from species typical of pastures in southern Finland. The species were *Geotrupes stercorarius* (Linnaeus, 1758), a large-bodied species which tunnels as an adult under dung pats; *Aphodius erraticus* (Linnaeus, 1758), a small-bodied species which lives as an adult within dung pats and whose larvae dig tunnels beneath them; *Aphodius pedellus* (De Geer, 1774), a small-bodied, dung-dwelling species; and

Aphodius fossor (Linnaeus, 1758), a relatively large, dung-dwelling species (Figure 1 and Appendix S1: Table S1). Based on previous work on temperate dung beetle communities, we predicted that *G. stercorarius* would have most influence on functioning, relative to the smaller *Aphodius* species (Rosenlew and Roslin 2008, Kaartinen et al. 2013, Nervo et al. 2014). We also expected different species to modify the functional effect of each other (Lähteenmäki et al. 2015), and the functional efficiency of species to change with a change in the environment (Slade and Roslin 2016). Tunnelling species (*G. stercorarius* and *A. erraticus*) are expected to contribute strongly to bioturbation of dung and soil, facilitating decomposition of dung, recycling of nutrients between dung and plants, and microbial activity (Slade et al. 2015, Slade and Roslin 2016). Small-bodied species living within dung pats (*A. pedellus* and *A. fossor*) are expected to contribute to the aeration of the pats, thus lowering fluxes of the greenhouse gas methane, which are greatest under anaerobic conditions (Penttilä et al. 2013, Slade et al. 2016). However, these predictions derive from measures of a single functions under average, uniform conditions.

2.2. Experimental design

We tested the individual and combined effects of the four species on functioning using the simplex response-surface design (Cornell 2002, Kirwan et al. 2009), creating 15 community types in total (four monocultures, six 2-species, four 3-species, and one 4-species mixture: Appendix S1: Figure S1). Rather than standardising overall biomass, we varied the abundance of each species within the range typically observed in nature (Roslin 2000, Roslin and Koivunen 2001, Rosenlew and Roslin 2008). To explore the sensitivity of our results to beetle density we repeated each of the 15 community types at two levels of initial beetle abundance (Appendix S1: Table S1). To get a measure of error, and as variance may not be constant across mixtures, we replicated community structure at the extremes of the experiment. Thus, we had three replicates of each of the monocultures at the low abundance level, and three replicates of the centroid at the high abundance

level. To assess ecosystem functioning in the absence of dung beetles, we established three mesocosms with dung pats but with no beetles, and three with no dung pat or beetles. Thus, in total we had 46 mesocosms that did not receive the increased precipitation treatment (see below). To explore how biodiversity–functioning relationships change when the system is perturbed, we simulated increased precipitation in a subset of the experimental communities (monocultures, 2-species, and 4 species mixtures at the two abundances, and six no dung beetle mesocosms: 28 mesocosms in total in the precipitation treatment) The precipitation treatment was scaled to match predicted increases in summer precipitation, and followed a watering regime similar to that used by (Vessby 2001) (see Appendix S1 for further details). Thus, the total number of mesocosms was 74.

2.3. Practical implementation

Experimental communities of dung beetles were established in Helsinki, Finland (for full details, see Appendix S1). Mesocosms were constructed from plastic buckets with their bases removed and dug 20 cm into a grass sward. To prevent beetles escaping, the tops of the mesocosms were covered with environmental mesh. The mesocosms were laid out in a grid pattern, with treatments and species mixtures randomized across the grid. Living dung beetles were collected from pastures in SW Finland between 5th and 7th June 2012 and added to the mesocosms – along with fresh dung (collected immediately upon defecation inside a barn, and so free from beetles) – on 8th June 2012. The experiment was run for 60 days, corresponding to the approximate larval development time of the species included (Roslin 2000). Mesh tops were removed after 20 days, as by this time the dung is drying out and no longer attractive to adult dung beetles (which feed on the liquid fraction of the dung) (Holter 1982). Thus, beetles were allowed to disperse naturally from the mesocosms, rather than constraining them to the pats for an unrealistic period of time (cf. Roslin 2000). Vegetation inside the mesocosms was regularly trimmed by hand.

2.4. Measurement of ecosystem functions

We measured multiple ecological function measures associated with five ecosystem functions: decomposition of dung, recycling of nutrients between dung and plants, fluxes of greenhouse gases from dung pats, and microbial activity of dung and soil (these are briefly described below with further details in Appendix S1).

Dung decomposition – We weighed dung pats in each mesocosm (wet mass, g) every 10 days. At the end of the experiment, we also dried and weighed all remaining dung to get a final dry mass.
Plant productivity – At the end of the experiment, we harvested all grass within the mesocosm. The grass was dried and weighed. We also extracted all soil from beneath each dung pat to a depth of 5 cm, homogenized it, placed a subsample in a pot and seeded it with ryegrass. After three weeks, the resultant grass was harvested and dried, and above-ground biomass recorded.

Nutrient content – We measured the ratio of carbon to nitrogen (C/N) in three substrates at the end of the experiment: the grass sampled in the mesocosms, the grass grown in pots, and the soil underneath the pats. For grazing animals, a lower C/N ratio in plants is expected to reflect higher protein content, higher palatability and thus better fodder quality. From a plant perspective, a lower C/N ratio in the soil is expected to reflect an increased availability of nitrogen, which is an essential element for plant growth.

Greenhouse gas fluxes – Fluxes of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) were measured using a closed chamber method (see Penttilä et al. 2013, Slade et al. 2016), and quantified using gas chromatography. Samples were taken on days 3, 6, 10, 15, 20, 30, 40, and 60. Fluxes of CO_2 from dung represent a secondary concern in terms of greenhouse effects, relative to

CH_4 and N_2O, so we down-weighted the relative importance of CO_2 (See Appendix S1, Table S2; (Penttilä et al. 2013)).

Microbial community structure and functioning – We recorded effects on the microbes of both the dung pat itself and the soil underneath it, by sampling each of these substrates at the early, mid- and late phase of the experiment. Microbial community composition was resolved by the LH-PCR method (2011), scoring overall microbial diversity. Substrate use was quantified using Biolog Ecoplates, and described by the inverse of the Simpson Index of substrates showing microbial growth within each substrate category (see Slade et al. 2015 for further details).

2.5. Statistical models

2.5.1. MULTIVARIATE ANALYSIS OF ECOLOGICAL RESPONSES

To model the ecological responses as functions of community composition we used the Multivariate Diversity-Interactions framework (Dooley et al. 2015). This approach tests how multiple ecosystem functions are simultaneously driven by species abundances, identities, interactions, composition, richness and evenness. It also enables the relative importance of those drivers to be tested, and allows identification of key species and interactions across multiple functions. The ecological function measures were modelled as a function of species effects (i.e. main effects of species-specific abundance) and the possible interactions between each species (i.e. two-, three-, and four-way interactions) (Appendix S1: Figure S1). The diversity-interaction model was re-parameterised to include the control mesocosms (containing dung but no beetles) as an intercept. This allows the species-specific effects to be interpreted as the deviation in function from the control. To assess whether the effects are altered by total abundance, we included interactions with abundance and all other model terms (See Appendix S1 for full details of the model).

The environmental perturbation (experimentally increased precipitation) is included in the model in a similar way to abundance, both as a main effect (a two-level categorical effect: ambient and elevated precipitation), and in interactions with species identity and species interaction terms. Here, the interactions capture the extent to which precipitation modifies both species-specific functional efficiency and interactions between species.

To determine the complexity of interaction terms required for the multivariate model, model fit was tested using F-tests, with sets of effects tested by comparing the fit of models including or excluding the terms. The minimum adequate model was the model with species effects, two-way interactions between species, and their interactions with abundance (Appendix S2: Table S1). The most complex species interactions found to be significant in the models involved pairs of species. Higher order (three- and four-way) species interactions were non-significant for all responses (Appendix S2: Table S1). The model selected was fitted to 16 ecological functions together using multivariate regression, assuming that residuals follow a multivariate normal distribution. This analysis tests whether the species-specific and interaction effects explain significant variation across all functions. It offers an important control over family-wise Type I errors. Crucially, the multivariate regression incorporates correlations between functions and provides unbiased estimates of the regression coefficients (as reported in Table 1). All models were fitted in SAS for Windows version 9.3, using the GLM procedure (SAS Institute Inc., Cary, NC, USA).

2.5.2. Analysis of Multifunctionality – Desirability Function Approach

As a complement to the function-specific analyses, we examined the extent to which individual species and species mixtures contribute to the desired state of overall ecosystem functioning. In this approach, the estimated ecological function responses $(\hat{y}_i,...,\hat{y}_f)$ from the multivariate regression

model are mapped to a desirability scale (d_1, d_2, …, d_f) using a desirability function. This mapping serves multiple purposes. First, it transforms the estimated ecological function responses from their scale of measurement (which may differ across functions) to a single comparable scale. Second, it may be optimal to maximize some functions, minimize others, or there could be an optimal target level for some. For each ecological function response y_i, a desirability function assigns numbers between 0 and 1, with $d_i = 0$ representing a completely undesirable value of y_i and $d_i = 1$ representing a completely desirable or ideal function value (for details on desirability functions, see Appendix S1 and Derringer and Suich (1980)). Finally, given that the f desirability responses d_1,…, d_f are on a scale from 0 to 1, they can be combined to give weighted multifunctionality, D.

One way to combine d_1,…, d_f is to take the weighted geometric mean, which has the property that if any one ecosystem function is completely undesirable (d_i=0), the overall multifunctionality is then also unacceptable (D=0). The geometric mean is weighted by the importance of the ecosystem function, with larger values corresponding to more important responses and smaller values to less important responses. The selection of importance weightings is subjective, and the determination of relative importance of functions may change depending on the stakeholder focus. In this study, there were five different ecosystem functions (dung decomposition, plant productivity, nutrient content, greenhouse gas fluxes and microbial activity, Figure 1, Appendix S1: Table S2). Rather than apply the weights individually to the 16 ecological function measures, we assigned importance across the five ecosystem functions. This also prevented over-weighting functions that had more ecological function measures. Within each ecosystem function, this overall importance was then distributed across individual ecological function measures (with the exception of greenhouse gas fluxes (see Figure 1, Appendix S1: Table S2)). Four ecosystem functions were unequivocally desirable in the context of agro-ecosystems for multiple stakeholders (e.g. farmers, society): maximizing *rates of dung decomposition* will reduce pasture soiling;

maximizing *plant productivity* and *plant nutrient content* will increase the quantity and quality of forage for livestock, and minimizing *greenhouse gas fluxes* will lower the impact of agriculture on climate change. It is less clear whether the fifth function, *diversity of the microbial community*, is desirable, as microbial activity may for example, simultaneously increase dung decomposition, but stimulate increased greenhouse gas fluxes. We therefore ran the analysis both including and excluding microbial activity measures and CO_2 fluxes from the overall multifunctionality analysis. As the results remained qualitatively unchanged, we present the results from the full analysis in the Results.

To examine how the valuation of ecosystem functions affects optimal multifunctionality we assessed overall multifunctionality for three contrasting scenarios where ecosystem services are weighted to reflect different societal preferences (e.g. Allan et al. 2015) (Appendix S1: Table S2). In the first scenario, each ecosystem function was treated as having equal importance, with a weighting of 1 assigned to each. In the second scenario, we placed a greater weight on the functions relating to the grass growth cycle (Appendix S1: Table S2, plant productivity = 5 and dung decomposition = 2), perceived as important for farmers. The weights for the other ecosystem functions remained at 1 for this scenario. In scenario 3, we placed a greater weight on the functions relating to minimising greenhouse gases (Appendix S1: Table S2, greenhouse gases = 5), while holding the importance for all other functions at 1. In addition, for scenario 3 we imposed upper limits on the desirability functions for the greenhouse gas functions. The limits chosen for each greenhouse gas were the maximum recorded value for the gas minus 20% of the range, i.e. the greenhouse gas fluxes must be below 80% of the range of the flux (e.g. for methane the maximum value was 3.19 g m^{-2} d^{-1} and the minimum -0.04 g m^{-2} d^{-1}. Thus, the upper limit imposed for methane was 2.55 g m^{-2} d^{-1}; a 20% reduction in the actual maximum values recorded. Thus, a community of beetles where methane was produced above this amount was not

considered desirable, D=0). Having obtained the weighted multifunctionality, D, for each scenario, univariate numerical optimisation techniques were then applied to D to obtain particular species relative abundances that optimized the multiple ecosystem functions. (i.e. to maximise the value of the overall multifunctionality measure D), we used the response optimiser tool for mixture experiments in Minitab Statistical Software version 17 (Minitab Inc., State College, PA). All models were fitted in SAS, procedure GLM (SAS Institute Inc., Cary, NC, USA). SAS code used for these analyses are available in the Supporting Information (Data S1). Data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.650fk.

3. Results

3.1. Response-specific results

Dung beetle community composition affected the full range of ecological functions (Figure 2, Table 1). Significant interactions between species were widespread but varied across responses (Table 1, Appendix S2: Table S1), often causing the functional efficiency of one species to shift substantially with a shift in the abundance of another (Figure 2, Table 1), clearly highlighting the complementarity in the system. When examined at the level of individual responses, individual species contributed unevenly, with an increasing abundance of any given species yielding higher rates of some functions but non-significant impacts or even lowered rates of others (Figure 2; Table 1). Impacts were qualitatively consistent across abundance levels (Table 1). *G. stercorarius* contributed positively to dung decomposition and methane reduction and interacted with *A. erraticus* species to increase grass growth, and *A. fossor* to increase dung removal, highlighting complementarity effects between species (Table 1, Appendix S2: Table S2). However, our prediction that it would contribute disproportionately to ecosystem functioning was not supported (Figures 2 and 3, Table 1). In contrast, *A. fossor* abundance was associated with decreased methane production, increased microbial diversity and enhanced dung decomposition (Figure 2, Table 1).

3.2. Perturbation by increased precipitation

Whilst there was an overall main effect of a simulated increase in precipitation on some functions, there was no consistent effect of this perturbation on the functional effects of species or interactions between them (Appendix S2: Table S3).

3.3. Multifunctionality and desirability analysis

When different ecosystem functions were weighed together into an overall multifunctionality function, *D*, different species and species interactions were important depending on the scenarios reflecting the different societal preferences (Figure 3). Under scenario 1, where each ecosystem function was treated as having equal importance (Figure 3a), optimal functioning was achieved by a community dominated by a single species, *A. fossor* (the highest values of *D* were always achieved with high abundances of *A. fossor* in the community). Maximum multifunctionality (*D*=0.57) was achieved in a high abundance community with species present in the proportions 93% of *A. fossor*, 6% of *A. erraticus*, *1% of G. stercorarius*, and 0% of *A. pedellus*, indicating dominance in the system. The desirability value of dung inhabited by this community was substantially higher than that achieved in the absence of dung beetles (*D* value of the control with dung but no beetles equalled 0.41). However, when *A. fossor* was absent all the three other species were needed in roughly equal proportions to achieve a similar level of functioning (Figure 3a, lower left panel: highest values of *D* in the centre of the triangle; Appendix S2: Table S2 and Table 1 show significant interactions between species other than *A. fossor*). Thus, under this scenario, maximal diversity, and high complementarity is needed to maintain functioning if the dominant species is lost.

In contrast, in scenario 2, with grass production functions more heavily weighted (Figure 3b), maximum multifunctionality (*D*=0.53) was achieved by a complementarity between two species in the proportions 60% *A. fossor* and 40% of *A. erraticus* (*D*=0.2 for the control dung

with no beetles). However, monocultures of *A. fossor* also gave high levels of multifunctionality, while monocultures of *A. erraticus* (as well as *G. stercorarius*, and *A. pedellus*, and two-species mixtures of *G. stercorarius* and *A. pedellus*) were quite undesirable (D <0.25). In this scenario the loss of *A. fossor* could not be compensated for by the other species in the community, and maximum functionality was reduced to within D=0.35-0.4 (lower left triangle Figure 3b). However, it should be noted that overall multifunctionality was robust to small changes in species composition under both these scenarios, with D close to the maximum for a range of multispecies communities.

For scenario 3 (Figure 3c), where a reduction in greenhouse gas emissions was the priority, and where a minimum 20% reduction limit had also been imposed, maximum multifunctionality (D=0.45) was lower. It was achieved in a high abundance community with species present in the proportions 72% of *G. stercorarius*, 13% of *A. erraticus*, 10% of *A. fossor*, and 5% of *A. pedellus*. Having dung beetles in the dung was crucial to ecosystem multifinctionality when a reduction in greenhouse gas emissions was the priority (the D value of the control dung with no dung beetles exceeded the limit imposed and so was considered completely undesirable, D=0). No single species alone was important under this scenario, although communities with *G. stercorarius*, particularly in combination with *A. fossor*, gave the highest functioning (Figure 3c, top two triangles). Functioning was greatly reduced if either of these two species was missing. In particular, if *G. stercorarius* was missing functioning was greatly reduced, and could not be maintained by the other three species (Figure 3c, bottom right triangle). Thus, only a few of the communities could reduce greenhouse gas emissions by the 20% limit imposed (i.e. large areas in the contour plots were considered completely undesirable (coloured blue), where the greenhouse gas emissions were above the upper allowable limit).

4. Discussion

Recent research has switched from studies focusing on the relationship between biodiversity and single ecological functions to studies considering multiple functions at the same time (Hector and Bagchi 2007, Gamfeldt et al. 2008, Bradford et al. 2014, Byrnes et al. 2014, Wagg et al. 2014, Allan et al. 2015, Lefcheck et al. 2015). We measured a range of ecological functions mediated by dung beetles and found that different species contribute unequally to individual functions. By combining two analysis frameworks, we were able to show that both species identity and species interactions are important for multifunctionality. While under some scenarios there appeared to be dominance in the system, this was dependent on the function, or combination of functions desired, and in some cases complementarity among species provided the highest ecosystem functioning (e.g. greenhouse gases Fig. 3c or when the dominant species was removed Fig. 3a, bottom left triangle). This highlights the importance of a multifunctionality perspective for a complete assessment of species' functional contributions, and crucially shows how multiple aspects of biodiversity can simultaneously drive ecosystem functioning.

4.1. All animals are equal, but are some more equal than others?

Higher levels of biodiversity are thought to be needed to maintain multiple ecosystem processes at multiple locations and times than a single process at a single location and time (e.g. Hector and Bagchi 2007, Isbell et al. 2011, Cardinale et al. 2012, Lefcheck et al. 2015, Butterfield et al. 2016). While this intuitively attractive hypothesis has been observed in some systems (e.g. Gamfeldt et al. 2013, Wagg et al. 2014, Perkins et al. 2015), other studies have found that single species may be more important than species richness, and that these functionally important species may be rare, common, or dominant within the system (e.g. Smith and Knapp 2003, Dangles and Malmqvist 2004, Hoey and Bellwood 2009, Allan et al. 2011, Winfree et al. 2015, Soliveres et al. 2016a).

The Multivariate Diversity-Interactions framework allowed us to assess how functions are affected by species interactions, and to examine the relative contributions of species under different scenarios. We found that optima for different functions were achieved with markedly different community structures (Figure 2), and that individual functions were generally not maximised by the same community composition that maximised multifunctionality (compare Figure 2 versus Figure 3). Previous work in both tropical (e.g. Larsen et al. 2005, Slade et al. 2007) and temperate (e.g. Rosenlew and Roslin 2008, Nervo et al. 2014) environments has suggested that large, tunnelling dung beetles are functionally dominant. However, we found no evidence of functional dominance by the large, tunnelling species *G. stercorarius*, although interactions between *G. stercorarius* and *A. fossor* were important for reducing greenhouse gas fluxes and increasing dung decomposition, as has been found in previous studies (Lähteenmäki et al. 2015, Slade and Roslin 2016).

Different species had clear and unequal contributions to particular functions, but one species, *A. fossor*, had a disproportionate effect on multiple functions under several scenarios. Despite this, if *A. fossor* was to go extinct, multifunctionality could often be maintained at a similar level through complementarity of the remaining species. These complementarity effects differed depending on the functions being maximised. When all functions were weighted equally, ecosystem multifunctionality was maintained without *A. fossor* if the remaining three species were retained in roughly equal proportions (Figure 3a). However, under a scenario where grass production functions were given higher weighting, maximum functioning was reduced when *A. fossor* was lost, and a two-species mixture of *G. stercorarius* and *A. erraticus* was most efficient (Figure 3b).

Dung beetle species partition their resources in both space and time (Holter 1982, Hanski and Cambefort 1991), with different breeding strategies allowing the use of dung of different ages (Gittings and Giller 1997, 1998). The presence of one species may therefore affect resource use by another. Monocultures of *A. erraticus*, *G. stercorarius*, and *A. pedellus* showed low levels of functioning in scenario 2, but functioning increased when *A. fossor* was present. This suggests that these species provide important indirect complementarity effects, which increase the functioning of *A. fossor*, perhaps through facilitation or niche partitioning. Similarly, in scenario 3, the complementarity effect between *G. stercorarius* and *A. fossor* was important for maximal functioning, and functioning was greatly reduced if either of these species was missing. Thus, while there appears to be both dominance and redundancy in the system, under changing conditions, complementarity allows functioning to be maintained. This highlights how, as predicted by theory (Gamfeldt et al. 2008, Tilman et al. 2014), multiple aspects of biodiversity can simultaneously drive ecosystem functioning.

These complementarity effects are perhaps unsurprising: if individual functions are optimized by different species, and different weightings are then given to different functions, we may expect different species combinations to be important. Indeed, when we weighted positively for grass production functions, the interaction between *A. erraticus* and *A. stercorarius* became important for maintaining multifunctionality in the absence of *A. fossor*. This two-species interaction was also important when grass growth was analyzed as a single function. Thus, optimizing multifunctionality is context-dependent, and is contingent on the weights chosen, and how stakeholders and society value the functions and services provided by biodiversity.

4.2. More species for more functions in more environments?

We found no significant effect of the precipitation treatment on the effects of species identity, or on interactions between species. Thus, the communities responded to perturbation in much the same way, irrespective of the abundance of individual species. The significant main effects of increased precipitation on some functions can be attributed to either physio-chemical effects, or to direct effects on the microbiome of the cow pats, without a role for dung beetles. While other studies have found that the importance of species identity for ecosystem functioning is at least partially mediated by environmental conditions (e.g. Isbell et al. 2011, Perkins et al. 2015), the lack of any detectable interactions between the environment and effects of species identity or species interaction implies a degree of resilience in this system to this level of perturbation, with functioning maintained under changing environmental conditions. Consistent with this, there was high resilience to species loss and changes in community composition and abundance, with overall multifunctionality remaining close to the maximum for a range of multispecies communities (Figure 3). However, we emphasize that our results also show that, as different species and species interactions were important under different scenarios reflecting the different societal preferences, high diversity may serve as a general insurance policy (Figure 3). Thus, other perturbations (e.g. increased temperatures, increased use of anthelmintics in farming systems, more variable precipitation events) may result in different species becoming increasingly important (Beynon et al. 2012, Dangles et al. 2012, Bartomeus et al. 2013, Lefcheck et al. 2015). The importance of species identity for ecosystem functioning appears to be highly context-dependent and contingent on the study system and/or environmental condition examined.

4.3. The importance of the Desirability Function Approach for BEF research

Weighted objective functions and thresholds have been used previously in the ecosystem services literature to consider trade-offs among multiple ecosystem services and land use scenarios (e.g. Polasky et al. 2008, Nelson et al. 2009, Duncan et al. 2015, Thompson et al. 2016). However, awareness of the need to define desirable functions under multiple scenarios is very recent in BEF research: such an approach is more likely to generate results that are useful to stakeholders and policy-makers (e.g. Byrnes et al. 2014, Duncan et al. 2015).

Our Desirability Function Approach allows us to investigate the effects of multiple drivers of biodiversity (species richness, species identity, and species interactions) on both individual functions and overall multifunctionality. In contrast to previous methods (e.g. Byrnes et al. 2014, Lefcheck et al. 2015) this method does not simply aggregate across the different species effects and trade-offs. Instead, we first apply a multivariate regression model (Dooley et al. 2015), which estimates all the species identity and interaction effects. Then, predicted values from this model are mapped onto a desirability scale using desirability functions. These functions can differ among the ecosystem functions, such that the researcher or stakeholder can decide whether it is optimal to maximimise, minimize, or reach a target value. These flexible functions also enable acceptable limits to be imposed on the function, and can therefore include weightings for functions that may negatively, as well as positively, affect ecosystem service delivery. These limits integrate the concept of thresholds (Byrnes et al. 2014, Duncan et al. 2015) into the single multifunction metric. The limits, or thresholds, can then be imposed across all ecosystem functions, or can differ among functions according to stakeholder focus. Thus, this approach enables trade-offs among ecosystem functions to be incorporated into BEF analyses (see also Allan et al. 2015), and BEF relationships to be scaled to final ecosystem service delivery and trade-offs (as called for by Duncan et al. 2015).

Our method of assigning weightings to functions and services according to perceived stakeholder values reveals that the optimal solution is contingent on the weights and limits chosen, i.e. the value placed on ecosystem services. Moreover, it highlights that the species required to maintain these services vary depending on the functions selected by the stakeholder. Thus, species perceived as redundant, or unnecessary for one function, may actually become important under changing scenarios. Both species identity and complementarity are therefore important if a full range of multiple functions and services are to be maintained.

4.3. Conclusions

While the past two decades have brought remarkable progress towards understanding how the loss of biodiversity affects the functioning of ecosystems, critical gaps remain. Recent studies have suggested that the next generation of BEF experiments should target three conceptual issues: the real complexity of species interactions, the non-random patterns characteristic of species loss, and the multiple mechanisms that may drive ecosystem functions across different contexts (Cardinale et al. 2012, Duncan et al. 2015). To predict the functional net effects of species turnover, we must understand which species are most important for functioning, and how sensitive they may be to perturbations (Suding et al. 2008, Oliver et al. 2015). Previous analytical tools have been unable to address these questions. By using two novel frameworks together (the Multivariate Diversity-Interactions framework and the Desirability Function Approach) we were able to assess how functions are affected by species interactions, and also to examine the relative contributions of species under different scenarios of species loss, environmental perturbation, and societal preferences. Our results highlight that understanding, managing, and optimizing ecosystem functioning requires multiple functions to be studied at the same time. From an ecosystem services perspective, whether single or multiple species will optimize ecosystem functioning is context-dependent, and will depend on the valuation of services by stakeholders and society.

Acknowledgements

We thank Esa Aaltonen for helping us design and build the experimental mesocosms, and Helena and Fredrik von Limburg Stirum for allowing us to collect dung beetles on their pastures. We thank John Finn and John Connolly for important input in the development of the statistical methodology. Bess Hardwick, Saija Lähteenmäki, Darren Mann, Atte Penttilä, Terhi Riutta, Minna Santalahti, and Asko Simojoki gave input into the design and implementation of the experiment, and Jarrett Byrnes, Laura Dee, and an anonymous reviewer gave constructive and encouraging comments, which greatly helped improve the manuscript. This study was funded by the Academy of Finland (grant 138346 to Tomas Roslin, Eleanor Slade, and Owen Lewis). EMS and LK would like to acknowledge joint first authorship of the manuscript. EMS, TB, OTL & TR designed the study, EMS performed the field research, LK, EMS, TB analyzed the data, and all authors contributed to the writing of the manuscript. We have no competing interests.

References

Allan, E., P. Manning, F. Alt, J. Binkenstein, S. Blaser, N. Blüthgen, S. Böhm, F. Grassein, N. Hölzel, V. H. Klaus, T. Kleinebecker, E. K. Morris, Y. Oelmann, D. Prati, S. C. Renner, M. C. Rillig, M. Schaefer, M. Schloter, B. Schmitt, I. Schöning, M. Schrumpf, E. Solly, E. Sorkau, J. Steckel, I. Steffen-Dewenter, B. Stempfhuber, M. Tschapka, C. N. Weiner, W. W. Weisser, M. Werner, C. Westphal, W. Wilcke, and M. Fischer. 2015. Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. Ecology Letters **18**:834-843.

Allan, E., W. Weisser, A. Weigelt, C. Roscher, M. Fischer, and H. Hillebrand. 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. Proceedings of the National Academy of Sciences **108**:17034-17039.

Andresen, E. 2002. Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. Ecological Entomology **27**:257-270.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters **9**:1146-1156.

Bang, H. S., J.-H. Lee, O. S. Kwon, Y. E. Na, Y. S. Jang, and W. H. Kim. 2005. Effects of paracoprid dung beetles (Coleoptera : Scarabaeidae) on the growth of pasture herbage and on the underlying soil. Applied Soil Ecology **29**:165-171.

Bartomeus, I., M. G. Park, J. Gibbs, B. N. Danforth, A. N. Lakso, and R. Winfree. 2013. Biodiversity ensures plant–pollinator phenological synchrony against climate change. Ecology Letters **16**:1331-1338.

Bell, T., J. A. Newman, B. W. Silverman, S. L. Turner, and A. K. Lilley. 2005. The contribution of species richness and composition to bacterial services. Nature **436**:1157-1160.

Beynon, S. A., D. J. Mann, E. M. Slade, and O. T. Lewis. 2012. Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems. Journal of Applied Ecology **49**:1365-1372.

Beynon, S. A., W. A. Wainwright, and M. Christie. 2015. The application of an ecosystem services framework to estimate the economic value of dung beetles to the UK cattle industry. Ecological Entomology **40**:124-135.

Bradford, M. A., S. A. Wood, R. D. Bardgett, H. I. J. Black, M. Bonkowski, T. Eggers, S. J. Grayston, E. Kandeler, P. Manning, H. Setälä, and T. H. Jones. 2014. Discontinuity in the responses of ecosystem processes and multifunctionality to altered soil community composition. Proceedings of the National Academy of Sciences **111**:14478-14483.

Butterfield, B. J., A. L. Camhi, R. L. Rubin, and C. R. Schwalm. 2016. Tradeoffs and compatibilities among ecosystem services: biological, physical and economic drivers of multifunctionality. Advances in Ecological Research **54**:207-243.

Byrnes, J. E. K., L. Gamfeldt, F. Isbell, J. S. Lefcheck, J. N. Griffin, A. Hector, B. J. Cardinale, D. U. Hooper, L. E. Dee, and J. E. Duffy. 2014. Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. Methods in Ecology and Evolution **5**:111-124.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature **486**:59-67.

Cornell, J. A. 2002. The Analysis of Mixture Data. Pages 223-285 Experiments with Mixtures. John Wiley & Sons, Inc.

D'hondt, B., B. Bossuyt, M. Hoffmann, and D. Bonte. 2008. Dung beetles as secondary seed dispersers in a temperate grassland. Basic and Applied Ecology **9**:542-549.

Dangles, O., C. Carpio, and G. Woodward. 2012. Size-dependent species removal impairs ecosystem functioning in a large-scale tropical field experiment. Ecology **93**:2615-2625.

Dangles, O., and B. Malmqvist. 2004. Species richness-decomposition relationships depend on species dominance. Ecology Letters **7**:395-402.

Dee, L. E., S. J. Miller, L. E. Peavey, D. Bradley, R. R. Gentry, R. Startz, S. D. Gaines, and S. E. Lester. 2016. Functional diversity of catch mitigates negative effects of temperature variability on fisheries yields. Proceedings of the Royal Society B: Biological Sciences **283**.

Derringer, G., and R. Suich. 1980. Simultaneous Optimization of Several Response Variables. Journal of Quality Technology **12**:214-219.

Dooley, Á., F. Isbell, L. Kirwan, J. Connolly, J. A. Finn, and C. Brophy. 2015. Testing the effects of diversity on ecosystem multifunctionality using a multivariate model. Ecology Letters **18**:1242-1251.

Duncan, C., J. R. Thompson, and N. Pettorelli. 2015. The quest for a mechanistic understanding of biodiversity–ecosystem services relationships. Proceedings of the Royal Society B: Biological Sciences **282**.

Gagic, V., I. Bartomeus, T. Jonsson, A. Taylor, C. Winqvist, C. Fischer, E. M. Slade, I. Steffan-Dewenter, M. Emmerson, S. G. Potts, T. Tscharntke, W. Weisser, and R. Bommarco. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices.

Gamfeldt, L., H. Hillebrand, and P. R. Jonsson. 2008. Multiple Functions Increase The Importance Of Biodiversity For Overall Ecosystem Functioning. Ecology **89**:1223-1231.

Gamfeldt, L., T. Snall, R. Bagchi, M. Jonsson, L. Gustafsson, P. Kjellander, M. C. Ruiz-Jaen, M. Froberg, J. Stendahl, C. D. Philipson, G. Mikusinski, E. Andersson, B. Westerlund, H. Andren, F. Moberg, J. Moen, and J. Bengtsson. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat Commun **4**:1340.

Gittings, T., and P. S. Giller. 1997. Life history traits and resource utilisation in an assemblage of north temperate Aphodius dung beetles (Coleoptera: Scarabaeidae). Ecography **20**:55-66.

Gittings, T., and P. S. Giller. 1998. Resource Quality and the Colonisation and Succession of Coprophagous Dung Beetles. Ecography **21**:581-592.

Hanski, I., and Y. Cambefort, editors. 1991. Dung Beetle Ecology. Princeton University Press, Princeton, New Jersey.

Hector, A., and R. Bagchi. 2007. Biodiversity and ecosystem multifunctionality. Nature **448**:188-190.

Hoey, A., and D. Bellwood. 2009. Limited Functional Redundancy in a High Diversity System: Single Species Dominates Key Ecological Process on Coral Reefs. Ecosystems **12**:1316-1328.

Holter, P. 1982. Resource Utilization and Local Coexistence in a Guild of Scarabaeid Dung Beetles (Aphodius spp.). Oikos **39**:213-227.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O/'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature **486**:105-108.

Isbell, F., V. Calcagno, A. Hector, J. Connolly, W. S. Harpole, P. B. Reich, M. Scherer-Lorenzen, B. Schmid, D. Tilman, J. van Ruijven, A. Weigelt, B. J. Wilsey, E. S. Zavaleta, and M. Loreau. 2011. High plant diversity is needed to maintain ecosystem services. Nature **477**:199-202.

Isbell, F. I., D. A. Losure, K. A. Yurkonis, and B. J. Wilsey. 2008. Diversity–productivity relationships in two ecologically realistic rarity–extinction scenarios. Oikos **117**:996-1005.

Jenkins, G. J., J. M. Murphy, D. S. Sexton, J. A. Lowe, P. Jones, and C. G. Kilsby. 2009. UK climate projections: Briefing report. Met Office Hadley Center, Exeter.

Jonsson, M., O. Dangles, B. Malmqvist, and F. Guerold. 2002. Simulating species loss following perturbation: assessing the effects on process rates. Proceedings of the Royal Society B: Biological Sciences **269**:1047-1052.

Jylhä, K., K. Ruosteenoja, J. Räisänen, A. Venäläinen, H. Tuomenvirta, L. Ruokolainen, S. Saku, and T. Seitola. 2009. The changing climate in Finland: estimates for adaptation studies. ACCLIM project report 2009., Finnish Meteorological Institute,, Helsinki.

Kaartinen, R., B. Hardwick, and T. Roslin. 2013. Using citizen scientists to measure an ecosystem service nationwide. Ecology **94**:2645-2652.

Kirwan, L., J. Connolly, J. A. Finn, C. Brophy, A. Lüscher, D. Nyfeler, and M. T. Sebastiá. 2009. Diversity–interaction modeling: estimating contributions of species identities and interactions to ecosystem function. Ecology **90**:2032-2038.

Lähteenmäki, S., E. M. Slade, B. Hardwick, G. Schiffler, J. Louzada, J. Barlow, and T. Roslin. 2015. MESOCLOSURES – increasing realism in mesocosm studies of ecosystem functioning. Methods in Ecology and Evolution **6**:10.1111/2041-1210X.12367.

Larsen, T. H., N. M. Williams, and C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters **8**:538-547.

Lefcheck, J. S., J. E. K. Byrnes, F. Isbell, L. Gamfeldt, J. N. Griffin, N. Eisenhauer, M. J. S. Hensel, A. Hector, B. J. Cardinale, and J. E. Duffy. 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nat Commun **6**:6936.

Levy, P. E., A. Burden, M. D. A. Cooper, K. J. Dinsmore, J. Drewer, C. Evans, D. Fowler, J. Gaiawyn, A. Gray, S. K. Jones, T. Jones, N. P. McNamara, R. Mills, N. Ostle, L. J. Sheppard, U. Skiba, A. Sowerby, S. E. Ward, and P. Zieliński. 2012. Methane emissions from soils: synthesis and analysis of a large UK data set. Global Change Biology **18**:1657-1669.

Loreau, M., S. Naeem, and P. Inchausti, editors. 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford.

Maestre, F. T., J. L. Quero, N. J. Gotelli, A. Escudero, V. Ochoa, M. Delgado-Baquerizo, M. García-Gómez, M. A. Bowker, S. Soliveres, C. Escolar, P. García-Palacios, M. Berdugo, E. Valencia, B. Gozalo, A. Gallardo, L. Aguilera, T. Arredondo, J. Blones, B. Boeken, D. Bran, A. A. Conceição, O. Cabrera, M. Chaieb, M. Derak, D. J. Eldridge, C. I. Espinosa, A. Florentino, J. Gaitán, M. G. Gatica, W. Ghiloufi, S. Gómez-González, J. R. Gutiérrez, R. M. Hernández, X. Huang, E. Huber-Sannwald, M. Jankju, M. Miriti, J. Monerris, R. L. Mau, E. Morici, K. Naseri, A. Ospina, V. Polo, A. Prina, E. Pucheta, D. A. Ramírez-Collantes, R. Romão, M. Tighe, C. Torres-Díaz, J. Val, J. P. Veiga, D. Wang, and E. Zaady. 2012. Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. Science **335**:214-218.

Mikkonen, A., K. Lappi, K. Wallenius, K. Lindström, and L. Suominen. 2011. Ecological inference on bacterial succession using curve-based community fingerprint data analysis, demonstrated with rhizoremediation experiment. FEMS Microbiology Ecology **78**:604-616.

Nelson, E., G. Mendoza, J. Regetz, S. Polasky, H. Tallis, D. Cameron, K. Chan, G. C. Daily, J. Goldstein, and P. M. Kareiva. 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in Ecology and the Environment **7**:4-11.

Nervo, B., C. Tocco, E. Caprio, C. Palestrini, and A. Rolando. 2014. The Effects of Body Mass on Dung Removal Efficiency in Dung Beetles. PLoS ONE **9**:e107699.

Nichols, E., S. Spector, J. Louzada, T. H. Larsen, S. Amezquita, M. Favila, and The Scarabaeinae Research Network 2008. Ecological functions and ecosystem services of Scarabaeine dung beetles: a review. Biological Conservation **141**:1461-1474.

Oliver, T. H., M. S. Heard, N. J. B. Isaac, D. B. Roy, D. Procter, F. Eigenbrod, R. Freckleton, A. Hector, C. D. L. Orme, O. L. Petchey, V. Proença, D. Raffaelli, K. B. Suttle, G. M. Mace, B. Martín-López, B. A. Woodcock, and J. M. Bullock. 2015. Biodiversity and Resilience of Ecosystem Functions. Trends in Ecology & Evolution **30**:673-684.

Penttilä, A., E. M. Slade, A. Simojoki, T. Riutta, K. Minkkinen, and T. Roslin. 2013. Quantifying Beetle-Mediated Effects on Gas Fluxes from Dung Pats. PLoS ONE **8**:e71454.

Perkins, D. M., R. A. Bailey, M. Dossena, L. Gamfeldt, J. Reiss, M. Trimmer, and G. Woodward. 2015. Higher biodiversity is required to sustain multiple ecosystem processes across temperature regimes. Global Change Biology **21**:396-406.

Pilegaard, K. 2013. Processes regulating nitric oxide emissions from soils. Philosophical Transactions of the Royal Society B: Biological Sciences **368**.

Polasky, S., E. Nelson, J. Camm, B. Csuti, P. Fackler, E. Lonsdorf, C. Montgomery, D. White, J. Arthur, and B. Garber-Yonts. 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. Biological Conservation **141**:1505-1524.

Proulx, R., C. Wirth, W. Voigt, A. Weigelt, C. Roscher, S. Attinger, J. Baade, R. L. Barnard, N. Buchmann, F. Buscot, N. Eisenhauer, M. Fischer, G. Gleixner, S. Halle, A. Hildebrandt, E. Kowalski, A. Kuu, M. Lange, A. Milcu, P. A. Niklaus, Y. Oelmann, S. Rosenkranz, A. Sabais, C. Scherber, M. Scherer-Lorenzen, S. Scheu, E.-D. Schulze, J. Schumacher, G. Schwichtenberg, J.-F. Soussana, V. M. Temperton, W. W. Weisser, W. Wilcke, and B. Schmid. 2010. Diversity Promotes Temporal Stability across Levels of Ecosystem Organization in Experimental Grasslands. PLoS ONE **5**:e13382.

Rosenlew, H., and T. Roslin. 2008. Habitat fragmentation and the functional efficiency of temperate dung beetles. Oikos **117**:1659-1666.

Roslin, T. 2000. Dung beetle movements at two spatial scales. Oikos **91**:323-335.

Roslin, T., M. Forshage, F. Ødegaard, C. Ekblad, and G. Liljeberg. 2014. Nordens dyngbaggar. Hyonteistarvike TIBIALE, Oy, Helsingfors.

Roslin, T., and A. Koivunen. 2001. Distribution and abundance of dung beetles in fragmented landscapes. Oecologia **127**:69-77.

Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia **122**:297-305.

Slade, E. M., D. J. Mann, J. F. Villanueva, and O. T. Lewis. 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. Journal of Animal Ecology **76**:1094-1104.

Slade, E. M., T. Riutta, T. Roslin, and H. L. Tuomisto. 2016. The role of dung beetles in reducing greenhouse gas emissions from cattle farming. Scientific Reports **6**:18140.

Slade, E. M., and T. Roslin. 2016. Dung beetle species interactions and multifunctionality are affected by an experimentally warmed climate. Oikos:doi: 10.1111/oik.03207.

Slade, E. M., T. Roslin, M. Santalahti, and T. Bell. 2015. Disentangling the 'brown world' faecal-detritus interaction web: dung beetle effects on soil microbial properties. Oikos:10.1111/oik.02640

Smith, M. D., and A. K. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. Ecology Letters **6**:509-517.

Soliveres, S., P. Manning, D. Prati, M. M. Gossner, F. Alt, H. Arndt, V. Baumgartner, J. Binkenstein, K. Birkhofer, S. Blaser, N. Blüthgen, S. Boch, S. Böhm, C. Börschig, F. Buscot, T. Diekötter, J. Heinze, N. Hölzel, K. Jung, V. H. Klaus, A.-M. Klein, T. Kleinebecker, S. Klemmer, J. Krauss, M. Lange, E. K. Morris, J. Müller, Y. Oelmann, J. Overmann, E. Pašalić, S. C. Renner, M. C. Rillig, H. M. Schaefer, M. Schloter, B. Schmitt, I. Schöning, M. Schrumpf, J. Sikorski, S. A. Socher, E. F. Solly, I. Sonnemann, E. Sorkau, J. Steckel, I. Steffan-Dewenter, B. Stempfhuber, M. Tschapka, M. Türke, P. Venter, C. N. Weiner, W. W. Weisser, M. Werner, C. Westphal, W. Wilcke, V. Wolters, T. Wubet, S. Wurst, M. Fischer, and E. Allan. 2016a. Locally rare species influence grassland ecosystem multifunctionality. Philosophical Transactions of the Royal Society of London B: Biological Sciences **371**:10.1098/rstb.2015.0269.

Soliveres, S., F. van der Plas, P. Manning, D. Prati, M. M. Gossner, S. C. Renner, F. Alt, H. Arndt, V. Baumgartner, J. Binkenstein, K. Birkhofer, S. Blaser, N. Blüthgen, S. Boch, S. Böhm, C. Börschig, F. Buscot, T. Diekötter, J. Heinze, N. Hölzel, K. Jung, V. H. Klaus, T. Kleinebecker, S. Klemmer, J. Krauss, M. Lange, E. K. Morris, J. Müller, Y. Oelmann, J. Overmann, E. Pašalić, M. C. Rillig, H. M. Schaefer, M. Schloter, B. Schmitt, I. Schöning, M. Schrumpf, J. Sikorski, S. A. Socher, E. F. Solly, I. Sonnemann, E. Sorkau, J. Steckel, I. Steffan-Dewenter, B. Stempfhuber, M. Tschapka, M. Türke, P. C. Venter, C. N. Weiner, W.

W. Weisser, M. Werner, C. Westphal, W. Wilcke, V. Wolters, T. Wubet, S. Wurst, M. Fischer, and E. Allan. 2016b. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature **536**:456-459.

Suding, K. N., S. Lavorel, F. S. Chapin, J. H. Cornelissen, S. Diaz, E. Garnier, D. Goldberg, D. U. Hooper, S. T. Jackson, and M. L. NAVAS. 2008. Scaling environmental change through the community‐level: a trait‐based response‐and‐effect framework for plants. Global Change Biology **14**:1125-1140.

Thompson, J. R., K. F. Lambert, D. R. Foster, E. N. Broadbent, M. Blumstein, A. M. Almeyda Zambrano, and Y. Fan. 2016. The consequences of four land‐use scenarios for forest ecosystems and the services they provide. Ecosphere **7**.

Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and ecosystem functioning. Annual Review of Ecology, Evolution, and Systematics **45**:471-493.

Vessby, K. 2001. Habitat and weather affect reproduction and size of the dung beetle Aphodius fossor. Ecological Entomology **26**:430-435.

Wagg, C., S. F. Bender, F. Widmer, and M. G. A. van der Heijden. 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences **111**:5266-5270.

Winfree, R., J. W Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common species, not species richness, drives delivery of a real‐world ecosystem service. Ecology Letters **18**:626-635.

Yamada, D., O. Imura, K. Shi, and T. Shibuya. 2007. Effect of tunneler dung beetles on cattle dung decomposition, soil nutrients and herbage growth Grassland Science **53**:121-129.

Supplementary online material

Appendix S1. Supplementary methods.

Appendix S2. Supplementary results.

Metadata S1. Description of SAS code

Data S1. SAS code

Data Availability

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.650fk

Table 1. Parameter estimates for measures of individual ecological functions and overall multifunctionality (for the two scenarios) in response to dung beetle diversity. As the experiment was repeated at two levels of initial beetle abundance (Appendix S1: Table S1) and for multiple types of responses (Fig. 1), values are given separately for low abundances (sub-tables A and B) and high abundances (sub-tables C and D) for functions involving Dung decomposition, Plant productivity, and Nutrient contents (sub-tables A and C) versus Greenhouse gas fluxes and Microbial Activity (sub-tables B and D), respectively. For Microbial Activity, values of *D* refer to Simpson's diversity index. Values in bold are significant at the 5% level.

A) Low abundance

Response type	Dung decomposition		Plant productivity		Nutrient contents		
Ecological function	Log (cumulative mass dung) (g)	Dry mass dung loss (g)	Grass pots (g)	Grass meso (g)	C/N grass meso	C/N grass pot	C/N soil
Control	**10.47**	**35.74**	**1.801**	**4.725**	**12.39**	**14.82**	**7.781**
G. stercorarius	-0.11	**-78.99**	**-0.426**	0.689	2.01	0.60	-0.725
A. fossor	**-0.50**	**50.10**	-0.326	0.512	1.31	0.68	-0.183
A. pedellus	-0.05	1.42	-0.152	0.650	1.68	0.52	0.850
A. erraticus	-0.14	12.44	-0.170	1.309	**2.23**	1.32	-2.148
G. stercorarius × *A. fossor*	0.46	**172.14**	-0.388	2.173	2.34	6.42	1.049
G. stercorarius × *A. pedellus*	-0.48	148.30	0.895	-5.100	-3.08	2.77	14.982
G. stercorarius × *A. erraticus*	-0.81	**246.65**	0.940	-12.441	**-14.38**	-5.10	-3.399
A. fossor × *A. pedellus*	-0.24	-10.21	-0.995	-0.867	-2.21	5.78	-1.444
A. fossor × *A. erraticus*	0.57	145.62	-0.031	4.792	-10.07	3.11	5.163
A. pedellus × *A. erraticus*	0.17	21.40	-0.628	12.279	-0.06	9.27	7.300

B) Low abundance

Response type	Greenhouse gas fluxes			Microbial Activity					
Ecological function	Cumulative CO_2 ($g\ m^{-2}\ d^{-1}$)	Cumulative CH_4 ($g\ m^{-2}\ d^{-1}$)	Cumulative N_2O ($g\ m^{-2}\ d^{-1}$)	*D* soil	*D* dung	*1/D* dung Eco	*1/D* soil Eco	Eco CSUR dung	Eco CSUR soil
Control	**2195.5**	**2.748**	**0.477**	**0.883**	**0.906**	**0.931**	**0.934**	**4.606**	**10.08**
G. stercorarius	-334.6	**-1.006**	0.017	**0.028**	**-0.040**	-0.043	-0.020	-0.371	-4.33
A. fossor	235.5	-0.467	-0.339	**0.033**	-0.011	-0.056	-0.003	-2.266	-2.04
A. pedellus	-183.9	-0.458	-0.016	0.018	-0.018	-0.016	0.010	-0.704	1.08
A. erraticus	-176.4	-0.190	0.039	**0.025**	-0.017	-0.030	-0.001	0.927	-1.07
G. stercorarius × *A. fossor*	18.2	1.043	1.132	0.017	-0.039	0.125	-0.002	-2.894	4.12
G. stercorarius × *A. pedellus*	-851.8	1.804	-0.364	0.052	-0.053	0.148	-0.013	**19.562**	-12.87
G. stercorarius × *A. erraticus*	**1592.4**	-0.407	0.934	**-0.191**	-0.052	0.107	0.104	6.463	18.22
A. fossor × *A. pedellus*	782.8	0.350	0.628	0.004	0.167	0.020	0.085	-2.634	17.96
A. fossor × *A. erraticus*	**2288.4**	**3.252**	1.694	0.059	0.064	-0.146	0.075	-10.307	7.66
A. pedellus × *A. erraticus*	6.9	-0.052	-1.041	-0.042	0.125	0.037	0.013	7.026	-0.98

C) High abundance

Response type	Dung decomposition		Plant productivity		Nutrient contents		
Ecological function	LOG (CUMULATIVE MASS DUNG) (G)	DRY MASS DUNG LOSS (G)	GRASS POTS (G)	GRASS MESO (G)	C/N GRASS MESO	C/N GRASS POT	C/N SOIL
Control	**10.47**	**35.74**	**1.801**	**4.725**	**12.39**	**14.82**	**7.781**
G. stercorarius	**-0.44**	**49.23**	-0.148	0.802	2.25	1.71	-0.856
A. fossor	**-0.68**	**54.63**	-0.153	0.327	0.32	0.04	0.872
A. pedellus	0.05	36.03	-0.286	3.479	0.08	2.32	0.809
A. erraticus	**-0.32**	14.56	-0.404	0.641	-0.76	0.07	-0.114
G. stercorarius × *A. fossor*	0.01	-17.49	-0.535	-9.988	-3.98	6.55	-6.361
G. stercorarius × *A. pedellus*	-0.83	-30.29	-0.110	1.864	4.97	-3.36	-11.00
G. stercorarius × *A. erraticus*	0.44	-27.39	-0.659	**28.294**	4.19	2.49	9.369
A. fossor × *A. pedellus*	-1.08	75.62	0.017	-9.907	-6.74	-3.47	6.040
A. fossor × *A. erraticus*	-0.76	144.42	-0.612	0.243	1.47	5.93	7.458
A. pedellus × *A. erraticus*	-0.23	-3.78	0.133	-4.346	7.52	-10.51	2.098

D) High abundance

Response type	Greenhouse gas fluxes			Microbial Activity					
Ecological function	Cumulative CO_2 ($g\ m^{-2}\ d^{-1}$)	Cumulative CH_4 ($g\ m^{-2}\ d^{-1}$)	Cumulative N_2O ($g\ m^{-2}\ d^{-1}$)	*D* soil	*D* dung	*1/D* dung Eco	*1/D* soil Eco	Eco CSUR dung	Eco CSUR soil
Control	**2195.5**	**2.748**	**0.477**	**0.883**	**0.906**	**0.931**	**0.934**	**4.606**	**10.08**
G. stercorarius	-240.7	-0.328	0.025	**0.040**	-0.004	-0.025	0.019	0.679	5.34
A. fossor	-215.4	**-1.099**	-0.226	**0.028**	-0.010	0.001	-0.008	0.686	-6.36
A. pedellus	221.7	0.165	0.157	**0.049**	0.010	-0.011	0.015	0.261	4.17
A. erraticus	75.5	-0.385	0.339	**0.033**	-0.003	-0.040	0.011	-0.051	-3.08
G. stercorarius × *A. fossor*	-456.5	1.284	0.172	-0.039	0.043	-0.074	0.039	-1.470	4.66
G. stercorarius × *A. pedellus*	-796.4	-1.648	-1.277	-0.024	-0.028	-0.028	-0.085	-3.300	-20.61
G. stercorarius × *A. erraticus*	740.9	-1.114	-0.955	**-0.143**	0.169	0.264	0.021	17.396	5.25
A. fossor × *A. pedellus*	344.0	**2.783**	-0.294	0.015	-0.147	-0.204	0.012	-0.047	2.45
A. fossor × *A. erraticus*	-208.1	**-2.340**	-0.949	-0.042	**-0.303**	-0.054	0.034	4.747	14.88
A. pedellus × *A. erraticus*	-853.4	-1.023	-0.245	-0.032	0.158	-0.080	0.013	-7.966	-0.98

Figure legends

Figure 1. Dung beetle species included and ecological functions measured in the mesocosm experiment. Larval chambers within and below the dung pat (as outlined in species-specific colours) show differences in species' breeding habits with a potential impact on functional contributions, on resource partitioning, and on the link between resource use and species richness. Importantly, the activity of different species may positively or negatively affect or complement each other (arrows in red), thus generating a general association between species richness and functioning, interactive effects between functional effects of individual species, and an 'insurance' effect sustaining functioning under changing environmental conditions. As measures of functioning, we recorded multiple ecological functions associated with the decomposition of dung, the recycling of nutrients between dung and plants, the fluxes of greenhouse gases from dung pats*, and the microbial activity of dung and soil, respectively (with each ecosystem function represented by a blue arrow in the drawing, and specific ecological function measures listed within each type). From an ecosystem services perspective, we then categorised each ecological function as to whether maximising or minimising it would be desirable (as indicated by (+) or (-), respectively). *Due to resource constraints, greenhouse gas fluxes were not measured in the precipitation treatments; all other functions were. For full details on each function measured see Appendix S1. Dung beetle images by Göran Liljeberg.

Figure 2. Contour plots of estimated rates of selected ecological functions in response to species composition. Each triangle represents an outer surface of the design tetrahedron shown in Fig. 1, with the fourth species held at zero. The vertices represent monocultures, the edges joining vertices represent two-species mixtures and the interior of the triangle represents three-species mixtures. Predictions are given at an average level of abundance. A) cumulative weight (g) of dung (log_{10} scale); B) dry weight of dung loss (g); C) cumulative CH_4 (g m^{-2} d^{-1}); D) Simpson's index (*D*) of

microbial diversity in the soil. Note that in each panel, darker green values signal higher values. Thus, in A) and C), low numbers (light green or blue hues) will imply high functioning (with lower dung mass remaining and reduced methane emissions, respectively), whereas in B) and D), high number (i.e. dark green hues) will indicate higher functioning (with more dung removed and higher microbial diversity, respectively).

Figure 3. Contour plots of overall multifunctionality, *D*, in response to species composition. Each triangular contour plot represents a three-species outer surface of the tetrahedron shown in Fig. 1, with the fourth species held at zero. The vertices represent monocultures, the edges joining vertices represent two-species mixtures and the interior of the triangle represents three-species mixtures. Predictions are given at an average level of abundance. Darker green values signal higher values of *D*. a) Scenario 1 with equal-importance weighting assigned to each ecosystem function, b) Scenario 2 with greater weightings assigned to grass productivity responses, c) Scenario 3 with a greater weight on the functions relating to minimising greenhouse gases.